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# A Study of Blocking and Overshadowing in Filial Imprinting

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The occurrence of blocking and overshadowing in filial imprinting was investigated in junglefowl chicks (*Gallus gallus spadiceus*). When subjects were exposed to a novel object in the presence of a familiar one, imprinting on the novel object was impaired in one of two experimental groups (Experiment 1). When subjects were exposed to two objects from the beginning, imprinting on each object was impaired (Experiment 2). These results suggest that phenomena resembling blocking and overshadowing in conditioning may occur in imprinting. The fact that overshadowing was much more prevalent and convincing than blocking is discussed by referring to processes involved in the formation of internal representations. It is suggested that processes connecting these representations to the executive system of filial behaviour may follow the rules of associative learning.

Spalding (1954) reported that chicks, as soon as they are able to walk, will follow any moving object. Later, Lorenz (1935, 1937) reported that young precocial birds become socially attached to the first conspicuous object they encounter (under natural circumstances a member of their own species) and subsequently prefer it to other objects. This phenomenon is usually referred to as filial imprinting (Bateson, 1966; Bolhuis, 1991). When the imprinting object is present, a chick spends a considerable amount of time close to it, often emitting soft twitters. When the object is removed, eating, drinking, and comfort behaviour such as preening disappear, and shrill (distress) calling becomes the predominant activity (Kruijt, 1985).

Lorenz (1935) suggested that imprinting is not dependent upon external reinforcement such as food or warmth. This point has also been stressed by Sluckin and Salzen (e.g. 1961), who described imprinting as a form of perceptual learning (cf. Hall, 1991). However, several researchers have suggested that reinforcement is involved and have proposed an associative-learning interpretation of filial imprinting (see Bolhuis, de Vos, & Kruijt, 1990, for a recent review). These interpretations assume that neutral features of

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an object (e.g. shape and colour) acquire control over filial behaviour as a consequence of being paired with reinforcing stimulation. The model developed by Hoffman and co-workers (e.g. Hoffman and Ratner, 1973) supposes that movement or sound provides this reinforcing stimulation. It has been shown, however, that birds can imprint on objects that do not move or emit sounds (e.g. Eiserer, 1980; Gray, 1960). Recently, Bolhuis et al. (1990) suggested that reinforcement is inherently present when a young bird is exposed to a conspicuous object. Evidence in support of this suggestion is provided by operant-conditioning experiments showing that imprinting stimuli can act as reinforcers in visually naive domestic chicks and mallard ducklings (Bateson & Reese, 1968).

In 1990, de Vos and Bolhuis reported that in junglefowl chicks imprinting on a novel object is impaired when that object is presented together with an object to which the animal had been imprinted previously. This phenomenon resembles that of blocking in classical conditioning, in which prior conditioning to one element of a compound stimulus impairs conditioning to the other element (Kamin, 1969). Van Kampen (1993a, 1993b) replicated the results of de Vos and Bolhuis, this time using a design in which the familiar and the novel stimuli were counterbalanced. However, applying a comparable design to investigate the occurrence of overshadowing (Pavlov, 1927) resulted in half of the chicks strongly preferring the one object and the other half the other. Van Kampen (1993a) interpreted these results as showing that those of de Vos and Bolhuis (1990) were most probably due to selective orientation by the chicks. That is, since the two elements of the compound stimulus were about 20 cm apart, chicks may have orientated mainly to one of these, not noticing the other. The present study was aimed at reinvestigating the occurrence of blocking and overshadowing in filial imprinting, in a situation in which the probability of selective orientation is reduced by placing the elements of the compound stimulus only slightly apart (1.6 cm).

## EXPERIMENT 1

This experiment examined the occurrence of blocking in filial imprinting. Subjects were first exposed to a blue, a red or a yellow object, and subsequently to the blue and the red object simultaneously.

### Method

*Subjects.* The subjects were 59 junglefowl chicks (*Gallus gallus spadiceus*) from three different batches of eggs, obtained from the laboratory breeding population (see Kruijt, 1964). The birds were hatched in individual compartments in a dark incubator maintained at 37.7°C.

*Exposure Conditions.* Between 8 and 18 hr after hatching, each chick was placed into a cage measuring 50 × 50 × 50 cm. The floor and the two side walls of the cage were made of wood, painted dark green; the rest of the cage was made of wire mesh. The cages were placed on a rack against a wall, facing a dark-brown screen at a distance of 1.5 m. Chicks could hear but not see each other. In the middle of each cage, a 40-W white light bulb (Philips "Softone"), suspended from the top, lit and heated the cage continuously. The temperature at floor level, 20 cm beneath the lamp, was approximately 30°C. Food was provided *ad libitum* on the floor in the middle of the cage. Water was also available *ad libitum* and was provided from a bottle at the front of the cage.

One imprinting object could be placed on either side of the midline of each cage, such that the objects were 1.6 cm apart and 9.5 cm away from the back of the cage. Three different objects were used, a blue one, a red one, and a yellow one. The blue and the red object consisted of 12 coloured wooden discs stacked on top of one another and fixed to the floor on a grey cylinder 1.5 cm high (diameter 2 cm). Discs were 1 cm high and either 6.0 cm (L) or 2.7 cm (S) in diameter. The blue object had the following configuration (top to bottom): L–2S–L–3S–L–3S–L, and the red object consisted of large discs only (12L). The yellow object was a cylinder with a pointed top. It was 12.5 cm high, had a diameter of 4.6 cm, and was fixed to the floor on a copper tube 2 cm high (diameter 1.2 cm). For an illustration of the objects the reader is referred to van Kampen (1993a).

The chicks were randomly divided into 3 groups, and they were exposed to one particular object for 7 days (Phase 1), and subsequently to the blue and the red object simultaneously (Phase 2). During the first phase, group B ($n = 19$) was exposed to the blue object, group R ($n = 20$) to the red object, and control group Y ($n = 20$) to the yellow object. The position of the objects in the cages (i.e. to the left or right of the midline) was randomized between chicks during both phases, except that in the experimental groups (B and R) the object present in Phase 1 was in the same position in Phase 2. During the changing of objects, which took about 5 min, chicks were placed into a test cage (see later) containing no objects. The first test was performed after 7 days of exposure in Phase 2, when the chicks were 14 days of age.

*Test Procedure.* Each chick was tested three times in a cage in a different room, also facing a dark-brown screen at a distance of 1.5 m. The tests were performed 7, 8, and 9 days after the change of objects in the chicks' home cages, on Days 15 to 17 of the experiment—Day 1 being the day of hatching. The test cage was similar to the chicks' home cages, except that one or both objects were absent. At the beginning of a test, a chick was placed into the middle of the front half of the test cage, and subsequently the number of shrill (*distress*) calls (Kruijt, 1985) was recorded during a 5-min period. On Days 15 and 16, the chicks received a test with either the blue or the red object present, and on Day 17 they were tested in a cage without objects (empty cage). The colour of the object presented on Day 15 was randomized between chicks, and on Day 16 they were tested with the alternative colour. During tests, objects were placed in the same position as in the home cage of the chick.

Strong attachment of chicks to an object should be apparent as a low frequency of shrill (distress) calling in the presence of that object (Hoffman, Ratner, & Eiserer, 1972; Kruijt, 1985). In order to obtain an index of the degree to which the presence of an object suppressed shrill calling and to reduce individual variation, a *calling ratio* was calculated for each chick, as follows: $O/(O + E)$, where $O$ = calling frequency when exposed to an object (blue or red), and $E$ = calling frequency in the empty cage. Before analysis, calling ratios were transformed using the arcsine transformation (Sokal & Rohlf, 1969).

## Results and Discussion

The mean calling ratios for the blue and the red object are presented in Figure 1. The occurrence of blocking should be apparent as a higher calling ratio for the blue object in the red group (R) compared to the blue object in the yellow control group (Y), and a higher calling ratio for the red object in the blue group (B) compared to the red object in the yellow control group (Y). A two-factor analysis of variance (ANOVA) with factors group (B, R, or Y) and object (blue or red) revealed that the difference between shrill calling with the blue and the red object varied significantly between groups (Group × Object: $F(1, 56) = 7.68, p < 0.01$). The amount of shrill calling with only the blue object

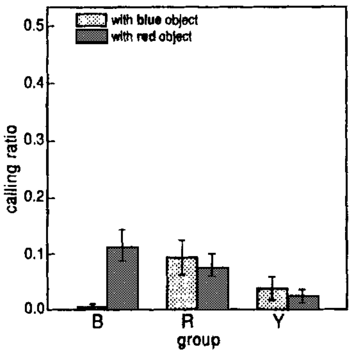


FIG. 1. Experiment 1: Mean calling ratio (±SE) for the blue and the red object, in the blue blocking group (B; $n = 19$), the red blocking group (R; $n = 20$), and the yellow control group (Y; $n = 20$).

also differed significantly between the three groups (ANOVA), $F(2, 56) = 5.16, p < 0.01$, as did the amount of calling with only the red object, $F(2, 56) = 3.82, p < 0.05$. More importantly, the calling ratio for the blue object was nearly significantly higher in the red group than in the yellow control group (Newman-Keuls: $p = 0.05$), and the calling ratio for the red object was significantly higher in the blue group than in the yellow control group, $p = 0.01$. Thus, consistent with the predictions regarding the effect of blocking, imprinting on the red object was impaired in the blue group, and there is a suggestion that imprinting on the blue object was impaired in the red group. Within the blue group, the calling ratio for the red object was higher than for the blue object (paired $t$-test), $t(18) = 3.94, p < 0.01$, but within the red group the calling ratio for the blue object was not significantly different from that for the red object, $t(19) = 0.41, p > 0.6$.

The fact that impaired imprinting was more convincing in the blue group may indicate that under these conditions the blue object is a more effective imprinting stimulus than is the red one. This suggestion receives confirmation in Experiment 2, which was in part performed simultaneously with Experiment 1. Indeed, using appetitive conditioning with rats, Feldman (1975) found that increasing the intensity of the added element may attenuate blocking.

## EXPERIMENT 2

This experiment examined the occurrence of overshadowing in filial imprinting. Subjects were exposed either to a blue and a red object simultaneously, or to only one of these.

### Method

*Subjects.* The subjects were 59 junglefowl chicks from three different batches of eggs, obtained from the laboratory breeding population. The birds were hatched in individual compartments in a dark incubator maintained at 37.7°C.

*Exposure Conditions.* Between 8 and 18 hr after hatching, each chick was placed into a cage measuring 50 × 50 × 50 cm, as described in Experiment 1. The animals were randomly divided into 3 groups. Control group B ($n = 20$) was continuously exposed to a blue object, control group R ($n = 19$) to a red object, and experimental group BR ($n = 20$) to both objects simultaneously. The objects were the same as those used in Experiment 1. The position of the objects in the cages, to the left or right of the midline, was randomized between the chicks.

*Test Procedure.* On Days 4 and 5, the chicks were exposed to the test cages (containing the same objects as were present in the home cages) in order to accustom them to the test procedure. There were two test series, one from Day 8 to Day 12 (Day 1 being the day of hatching) and a second from Day 15 to Day 17. In both series calling frequencies were measured following the procedure described in Experiment 1. On Days 8 and 12, chicks received a test in an empty cage, the results of which were averaged for each chick. On Day 9, all animals were tested with the same objects as in their home cage; chicks in the control groups (B and R) were also tested in this situation on Days 10 and 11. Chicks in the experimental group (BR) were tested with either the blue or the red object on Day 10. The colour of the object presented was randomized between the birds, and on Day 11 they received a test with the alternative colour. The position of an object in the test cage was always the same as its position in the subject's home cage.

The overshadowing effects in Test Series 1 turned out to be much more substantial and convincing than the blocking effect of Experiment 1. This might be due to the fact that chicks in the blocking experiment were older during testing than those in the overshadowing experiment and motivational processes may change during development. To allow for a better comparison between the two experiments, the second series of tests was performed on exactly the same days as in the blocking experiment and following exactly the same schedule. On Days 15 and 16, all chicks received a test with either the blue or the red object present, and on Day 17 they were tested in a cage without objects. The colour of the object presented on Day 15 was randomized between the chicks, and on Day 16 they were tested with the alternative colour. The position of the novel object in the test cage of the control groups—the blue object for the red group and the red object for the blue group—was opposite to where the training object was placed in the home cage.

## Results and Discussion

*Test Series 1.* The mean calling ratios of the experimental group for the blue and the red object are presented in Figure 2, together with the mean calling ratios of the control groups for their training object. The occurrence of overshadowing should be apparent as a higher calling ratio for the blue object in the experimental group (BR) than in the blue control group (B), and/or a higher calling ratio for the red object in the experimental group (BR) than in the red control group (R). Indeed, experimental chicks called more with the blue object than did chicks in the blue group, $t(38) = 4.61$, $p < 0.001$, and they also called more with the red object than did chicks in the red group, $t(37) = 6.49$, $p < 0.001$. Thus, consistent with the predictions regarding the effect of overshadowing, development of attachment to both objects was impaired in the experimental group.

Within the experimental group, calling ratios for the blue object, for the red object, and for both objects together differed significantly (ANOVA), $F(2, 38) = 12.96$, $p < 0.001$. Chicks called least when both objects were present and most with the red object (Newman–Keuls: $p < 0.05$, in all cases). The finding that calling with each object

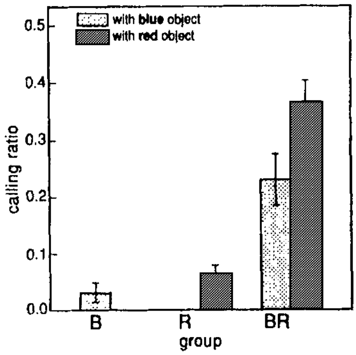


FIG. 2. Experiment 2, Test Series 1: Mean calling ratio ($\pm$SE) of the blue control group (B; $n = 20$) for the blue object, of the red control group (R; $n = 19$) for the red object, and of the experimental group (BR; $n = 20$) for either object.

separately was higher than with both objects present together is also consistent with the predictions regarding the effect of overshadowing. Furthermore, the finding that experimental chicks called more with the red object than with the blue one suggests that the latter object was indeed a more effective imprinting stimulus than was the former. This suggestion is confirmed by the results of the control groups, showing that over Days 9, 10, and 11, subjects trained with the blue object had significantly lower ratios than did those trained with the red object (two-factor ANOVA), $F(1, 37) = 8.15, p < 0.01$. There were no significant differences between calling ratios of the control groups over these three days, $F(2, 74) < 1, p > 0.7$; Day $\times$ Group, $F(2, 74) = 1.52, p > 0.2$. The finding that the blue object is a more effective imprinting stimulus is consistent with the results of the previous experiment, showing that imprinting was more strongly impaired after pre-exposure to the blue object than after pre-exposure to the red object.

*Test Series 2.* Mean calling ratios for the blue and the red object are presented in Figure 3 for all three groups. Again, the occurrence of overshadowing should be apparent as a higher calling ratio for the blue object in the experimental group (BR) than in the blue control group (B), and/or a higher calling ratio for the red object in the experimental group (BR) than in the red control group (R). A two-factor ANOVA with factors group (B, R, or BR) and object (blue or red) revealed a significant interaction between these factors, $F(2, 56) = 134.00, p < 0.001$, and therefore separate ANOVAs were performed on each test condition. There was a significant difference between the groups with respect to calling with the blue object, $F(2, 56) = 69.73, p < 0.001$, with chicks in the experimental group calling more than did those in the blue control group, but less than did chicks in the red control group (Newman–Keuls: $p < 0.01$, in all cases). The three groups also called differently with the red object, $F(2, 56) = 32.82, p < 0.001$, with experimental chicks calling more than did those in the red control group, but less than did chicks in the blue control group, $p < 0.01$, in all cases.

Thus, the results of Test Series 2 are consistent with those of Series 1 and show that in the experimental group attachment to both the blue and the red object was impaired.

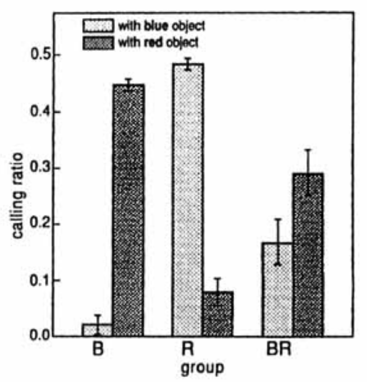


FIG. 3. Experiment 2, Test Series 2: Mean calling ratio (± SE) for the blue and for the red object, in the blue control group (B; $n$ = 20), the red control group (R; $n$ = 19), and the experimental group (BR; $n$ = 20).

These results are also consistent with the predictions regarding the effect of overshadowing. Furthermore, the results also show that the impairment was not complete, as experimental chicks called less with the red object than did chicks in the blue control group, and less with the blue object than did chicks in the red control group.

## GENERAL DISCUSSION

The aim of the present study has been to examine whether blocking and overshadowing may occur in filial imprinting. In 1990, de Vos and Bolhuis reported results suggesting that blocking may occur, but van Kampen (1993a) concluded that these findings were probably a consequence of selective orientation by the subjects during the blocking phase, in which the objects were about 20 cm apart. Therefore an attempt was made to reduce the probability of selective orientation in the present study by placing the objects only slightly apart (1.6 cm). Indeed, in one of two blocking groups development of attachment to a novel object was impaired in the presence of a familiar object (Experiment 1), and a phenomenon closely resembling reciprocal overshadowing was also observed (Experiment 2). The fact that during the overshadowing procedure subjects became attached to both objects, whereas attachment to each object was impaired, excludes the possibility that the present results are due to selective orientation.

In a selective orientation explanation it is assumed that subjects can imprint on each object but fail to do so because they orientate themselves in such a way that they receive more exposure to one than the other. For instance, in a previous overshadowing experiment with the elements of the compound imprinting stimulus presented about 20 cm apart, chicks became fully imprinted on only one object—either one or the other—whereas no attachment accrued to the other object (van Kampen, 1993a, 1993b). In that particular case chicks may have orientated to only one object during exposure, not noticing the other. However, as the present results reveal attachment to both objects, it must be assumed that subjects also attended to both objects. Thus, if it were still assumed that the impaired imprinting on each object is the result of selective orientation, it must be that the subjects did not orientate to either object long enough to become fully imprinted on it. This possibility can be discarded on the basis of what is known about filial imprinting. That is, imprinting is a very rapid process, which occurs within several hours (Bateson, 1966; Bolhuis, 1991). Therefore it would have to be assumed that chicks spent less than several hours looking at either object during the whole two weeks of continuous exposure in the overshadowing experiment, and thus spent most of their time looking away. This is contrary to what is known about the function and result of imprinting—namely, that subjects will always remain in close contact with their imprinting object (Andrew & Dharmaretnam, 1991; Bateson, 1966; Workman, Kent, & Andrew, 1991). Thus, even if chicks are assumed to divide their time between looking at one object and looking at the other, it must be predicted that they will spend enough time looking at each object in order to become fully imprinted on at least one of them.

The process in imprinting that might follow the rules of associative learning is the one connecting representations to the executive system of filial behaviour as proposed by Bateson (1987), or, in Timberlake's terminology, to the filial system (Timberlake & Lucas, 1989; see also Hogan, 1988). Indeed, recently Bateson and Horn (1994) presented a network model for imprinting in which the connection between the recognition system and the executive system is strengthened as a result of conjoint activity, and this is what is generally accepted to be the basis of all associative learning (e.g. Hebb, 1949). An additional explanation of the overshadowing results, which does not apply to blocking, is that they are due not only to processes connecting representations to the executive system, but also to the way in which these representations are built up. That is, if subsequent to training with two objects one configural unit is formed, as suggested by Pearce (1994), presentation of only one object during testing would lead to less responding because of generalization decrement between the training and the testing situation. Along with discrepancy models (Pearce & Hall, 1980; Rescorla & Wagner, 1972), generalization-decrement models have proved to be very successful in explaining the occurrence of overshadowing in conditioning (Pearce, 1987, 1994). The model developed by Pearce (1994) might also apply to the case of imprinting if it is assumed that configural units connect not to a US unit, as is suggested to be the case in conditioning, but to the executive system of filial behaviour. Evidence has already accumulated suggesting that the process of the formation of a representation is similar in conditioning and imprinting (Bateson & Horn, 1994; Bolhuis, 1991; Hollis, ten Cate, & Bateson, 1991; van Kampen, de Haan, & de Vos, 1994). The fact that overshadowing was much more prevalent and convincing than was blocking might be due to the characteristics of this process.

Recently, Honey et al. (Honey, Bateson, & Horn, 1994; Honey, Horn, & Bateson, 1993) have reported two studies investigating perceptual learning in imprinting. It was found that discrimination learning involving two relatively similar stimuli was enhanced after prior exposure to both stimuli (Honey et al., 1994; cf. Chantrey, 1974), but also after prior exposure to only one of the stimuli (Honey et al., 1993; cf Chantrey, 1972). Although no comparison was made between the two situations, previous research using a more conventional design has revealed that prior exposure to both stimuli produces faster discrimination learning than does prior exposure to one stimulus (Bennett, Levitt, & Anton, 1972). This result is also predicted by the model of Bateson and Horn (1994) and might be the basis of the incomplete impairment found in the blocking experiment.

McLaren, Kaye, and Mackintosh (1989) suggested that exposure to two stimuli will lead to latent inhibition of the common features. In an imprinting situation with two stimuli, A and B, consisting of features *ax* and *bx*, this might result in the common features *x* not becoming as strongly connected to the executive system of filial behaviour as the unique features *a* and *b*. In a blocking situation with prior exposure to Stimulus A, both *a* and *x* features will have become strongly connected to the executive system. Introduction of Stimulus B is then expected to evoke filial responses through generalization (Bolhuis & Horn, 1992; Cofoid & Honig, 1961; cf. Pearce, 1987), resulting in impaired discrimination learning compared to pre-exposure to both stimuli. Activation of the executive system through generalization may result in the unique features *b* gaining control over filial behaviour, and it could even be hypothesized that the common features *x* will gain additional associative strength. Thus, in the present overshadowing situation, chicks may have become relatively more attached to the unique features of the two objects, whereas in the blocking situation they may have become more attached to the common features. In the former situation transfer of attachment from one object to another during testing is minimized, augmenting the overshadowing effect, whereas in the latter situation generalization is much stronger, attenuating blocking.

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## Une étude du blocage et de l'"overshadowing" lors de l'empreinte filiale

L'occurrence du blocage et de l'"overshadowing" lors de l'empreinte filiale a été étudiée chez des poulets "junglefowl" (*Gallus gallus spadiceus*). Lorsque les sujets sont exposés à un nouvel objet en présence d'un objet familier, l'empreinte envers ce nouvel objet est détériorée chez l'un de deux groupes expérimentaux (Expérience 1). Lorsque les sujets sont mis en présence des deux objets dès le début, l'empreinte envers les deux objets est détériorée (Expérience 2). Ces données suggèrent que des phénomènes semblables au blocage et à l'"overshadowing" lors du conditionnement puissent survenir lors de l'empreinte. Le fait que l'"overshadowing" est nettement plus prédominant et convaincant que le blocage est discuté par rapport à des processus impliqués dans la formation de représentations internes. Il est suggéré que des processus connectant ces représentations au système exécutif du comportement filial suivent les règles de l'apprentissage associatif.

## Un estudio sobre el bloqueo y el ensombrecimiento en la impronta filial

En este estudio se intentó demostrar la existencia de bloqueo y ensombrecimiento en la impronta filial en pollos (*Gallus gallus spadiceus*). Cuando los sujetos eran expuestos a un objeto nuevo en presencia de otro familiar, la impronta hacia el objeto nuevo quedó disminuída en uno de dos grupos experimentales (Experimento 1). Cuando los sujetos eran expuestos desde el principio a los dos objetos, quedó disminuída la impronta hacia ambos (Experimento 2). Estos resultados indican que procesos semejantes al bloqueo y el ensombrecimiento, usuales en situaciones de condicionamiento, pueden también ocurrir en el aprendizaje por impronta. El hecho de que el ensombrecimiento fuera mucho más notorio y convincente que el bloqueo se interpreta en términos de los distintos procesos que intervienen en la formación de representaciones internas y se sugiere que los procesos que conectan estas representaciones con el sistema ejecutivo de la conducta filial podrían seguir las reglas del aprendizaje asociativo.